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Extending Levelt's Propositions to perceptual multistability involving interocular grouping: Experiment

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Abstract

Levelt's Propositions have been a touchstone for experimental and modeling studies of perceptual multistability. We asked whether Levelt's Propositions extend to perceptual multistability involving interocular grouping. To address this question we used split-grating stimuli with complementary halves of the same color (either red or green). As in previous studies, subjects reported four percepts in alternation: the two stimuli presented to each eye (single-eye percepts), as well as two interocularly grouped, single color percepts (grouped percepts). Most subjects responded to increased color saturation by more frequently reporting a single color image, thus increasing the predominance of grouped percepts (Levelt's Proposition I). In these subjects increased predominance was due to a decrease in the average dominance duration of single-eye percepts, while that of grouped percepts remained largely unaffected. This is in accordance with generalized Levelt's Proposition II which posits that the average dominance duration of the stronger (in this case single-eye) percept is primarily affected by changes in stimulus strength. In accordance with Proposition III, the alternation rate increased as the difference in the strength of the percepts decreased.

Keywords: Multistable perceptual rivalry, Levelt's propositions, interocular grouping

1. Introduction

We are remarkably adept at interpreting noisy and ambiguous visual inputs (Kersten et al., 2004; Fiser et al., 2010). However, sometimes competing interpretations of a stimulus are not disambiguated, and different interpretations are perceived in alternation. For example, binocular rivalry occurs when the two eyes are presented with disparate images. Instead of perceiving a fusion of the two images, one experiences intermittent switching between two distinct percepts (Wheatstone, 1838; Blake and Logothetis, 2002). Multistable perceptual phenomena have been used extensively to study visual awareness and its underlying cortical

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Preprint submitted to Vision Research

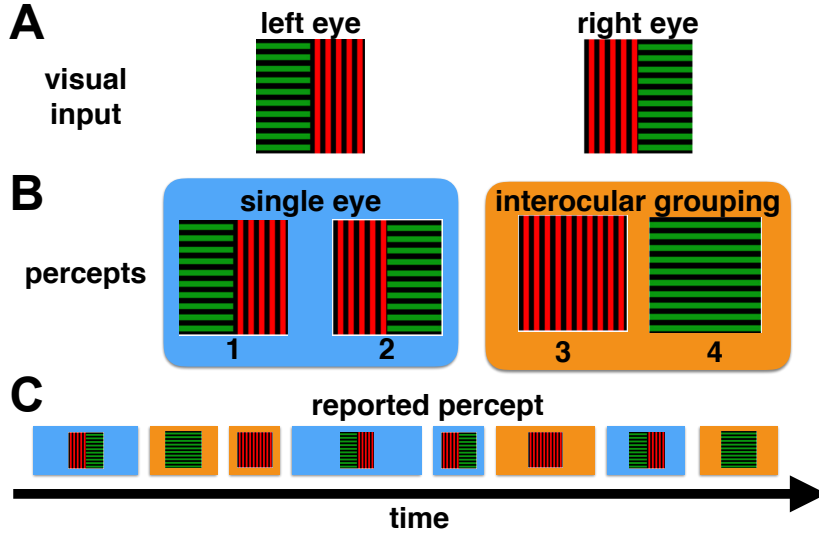


Figure 1: (A) An example of the stimuli presented to the left and right eyes. Gratings were always split so that halves with the same color and orientation could be matched via interocular grouping, but were otherwise randomized across trials and blocks (see Methods). (B) Subjects typically reported seeing one of four percepts – two single-eye and two grouped – at any given time during a trial. (C) A typical perceptual time series reported by a subject, showing the stochasticity in both the dominance times and the order of transitions between percepts.

39 mechanisms (Leopold and Logothetis, 1996; Polonsky et al., 2000; Tong et al., 2006; Sterzer
 40 et al., 2009).

41 Levelt’s observations (Levelt, 1965) have become a touchstone for experimental and mod-
 42 eling studies of perceptual rivalry (Blake, 1989; Moreno-Bote et al., 2007; Shpiro et al., 2007;
 43 Wilson, 2003; Said and Heeger, 2013; Seely and Chow, 2011). Levelt’s original Propositions
 44 relate *stimulus strength*, *predominance* (the fraction of time a percept is dominant), and *dom-*
 45 *inance durations* (the duration of the dominant percept) in bistable binocular rivalry (Bras-
 46 camp et al., 2015): (I) Increasing the stimulus strength of the stimulus presented to one
 47 eye increases the perceptual predominance of that stimulus; (II) Increasing the difference
 48 in stimulus strengths between the two eyes increases the perceptual dominance duration
 49 of the stronger stimulus; (III) Increasing the difference in stimulus strength between the
 50 two eyes reduces the perceptual alternation rate; (IV) Increasing stimulus strength in both
 51 eyes while keeping it equal between eyes increases the perceptual alternation rate. Levelt’s
 52 propositions also hold in other cases of bistable perceptual rivalry such as bistable rotating
 53 structure-from-motion (Klink et al., 2008), bistable ambiguous plaids (Moreno-Bote et al.,
 54 2010), and motion-induced blindness (Carter and Pettigrew, 2003; Bonnef et al., 2014).

55 However, whether Levelt’s propositions hold in the case of rivalry between more than
 56 two percepts is not clear. Such multistable rivalry can occur when multiple patches of two
 57 visual scenes are intermingled and the results presented to different eyes simultaneously. In
 58 this case, observers intermittently perceive the original, coherent scenes as well as the images
 59 presented to each single eye (Kovacs et al., 1996).

60 We hypothesized that Levelt’s propositions extend to perceptual multistability involv-

ing interocular grouping (Kovacs et al., 1996; Diaz-Caneja, 1928; Suzuki and Grabowecky, 2002). We divide percepts into two groups, the stimuli presented to each eye, and interocularly grouped percepts. Following Brascamp et al. (2015) we say that a stimulus parameter that affects a percept’s predominance affects its strength. Levelt’s Propositions generalize to: (I) *Increasing grouped percept strength increases the perceptual predominance of those percepts*; (II) *Increasing the difference between the percept strength of grouped and single-eye percepts increases the perceptual dominance duration of the stronger percepts*; (III) *Increasing the difference in percept strengths between grouped percepts and single-eye percepts reduces the perceptual alternation rate*; (IV) *Increasing percept strength in both grouped percepts and single-eye percepts while keeping it equal among percepts increases the perceptual alternation rate* (Brascamp et al., 2015). We use “percept strength” rather than Levelt’s original “stimulus strength,” as our manipulations affected the strength of percepts, rather than the separate stimuli presented to each eye.

To test this generalization of Levelt’s Propositions we used split-grating stimuli (See Fig. 1A) for which subjects reliably reported four percepts in alternation: single-eye percepts – the two stimuli presented to each eye (percepts 1 and 2 in Fig. 1B), as well as two interocularly grouped, single color percepts (3 and 4 in Fig. 1B). We hypothesized that an increase in color saturation increases the strength of the coherent, grouped percepts. Indeed, we found that for most subjects an increase in color saturation lead to increased predominance of grouped percepts (Proposition I). At the same time the dominance duration of single-eye (stronger) percepts decreased, while that of grouped (weaker) percepts remained largely unaffected (Proposition II). As a consequence, the alternation rate increased with a reduction in the difference of percept strengths (Proposition III). **A more detailed analysis showed that these effects are primarily due to the increased strength of all red percepts (4 in Fig. 1B).** In addition, we found that an increase in the predominance of grouped percepts was partly due to an increase in the fraction of visits to grouped percepts.

Color has been previously reported to affect interocular grouping (Kovacs et al., 1996). However, to our knowledge the changes in the predominance of grouped images due to changes in color saturation, and the corresponding extensions of Levelt’s propositions to multistable rivalry have not been studied previously.

2. Methods

2.1. Experiment

Observers. Nine observers with normal or corrected-to-normal vision, including three of the authors (AJ, ZK, YW), participated in this experiment. Six were naive to the experimental hypotheses and three were not. The experiments were conducted according to a protocol approved by the University of Houston Committee for the Protection of Human Subjects and in accordance with the federal regulations 45 CFR 46, the ethical principles established by the Belmont Report, and the principles expressed in the Declaration of Helsinki. All participants provided their written informed voluntary consent following the consent procedure approved by the University of Houston Committee for the Protection of Human Subjects. Data are presented for all nine subjects.

Apparatus. The visual stimuli used in the experiment were generated using a VSG visual stimulus generator card (VSG 2/5, Cambridge Research Systems). The stimuli were displayed on a calibrated 19” high resolution color monitor with a 100 Hz frame rate. Monitor

105 calibration was carried out using CRS colorCAL colorimeter. A head/chin rest was used to
106 stabilize observers' head position. The distance between the monitor and the observer was
107 set to 108 cm. We used a stereoscopic mirror arrangement (haploscope) in order to present
108 the left and right stimuli separately to the left and right eyes. It consisted of four mirrors,
109 whose horizontal/vertical positions and inclinations could be adjusted using screws.

110 *Stimuli.* Subjects were presented with variations of the stimulus depicted in Fig. 1A. A
111 square composed of two orthogonal gratings was presented to each eye using the haploscope.
112 The orthogonal gratings were arranged so that interocular grouping resulted in a percept
113 with single, i.e., uniform orientation (horizontal or vertical). In order to have a stimulus
114 parameter to control the percept strength for this interocular grouping, we have added color
115 to our stimuli, such that interocular grouping would lead not only to a uniform orientation
116 but also to a uniform color (Fig. 1A). Stalmeier and de Weert (1998) studied the contribution
117 of color and luminance contrast to binocular rivalry. In their experiments, the stimulus to
118 one eye was achromatic concentric rings whereas the stimulus to the other eye was a radial
119 pattern made of isoluminant color pairs. They showed that the dominance duration of the
120 colored radial pattern, hence the strength of the chromatic input, increased as the chromatic
121 distance, $d(u, v)$, between the colors in the CIE 1960 space increased up to $d(u, v) \approx 0.1$,
122 and saturated thereafter. There were also significant differences in dominance durations
123 depending on the criterion for isoluminance (flicker photometry vs minimal distinct border
124 (MDB) criterion), and the direction of change in the color space. Finally, their results showed
125 inter-subject variability both in the effectiveness of pure chromatic contrast and achromatic
126 contrast.

127 In preliminary observations, we found color saturation effectively controlled percept
128 strength for interocular grouping. Hence, grating halves were assigned a color – either
129 red or green – at two different saturation levels, 0.4 or 0.9. The HSV color space coordinates
130 for red and green were (0.497, 0.4/0.9, 0.7) and (120.23, 0.4/0.9, 0.7), respectively, with the
131 pair of values 0.4/0.9 referring to two different levels of color saturation. At low saturation
132 ($S = 0.4$), the corresponding CIE 1960 (u, v) coordinates for red were (0.214, 0.3) and
133 $L = 57.7cd/m^2$; whereas for green they were (0.169, 0.315) and $L = 72cd/m^2$. At high saturation
134 ($S = 0.9$), the corresponding CIE 1960 (u, v) coordinates for red were (0.333, 0.329)
135 and $L = 25.4cd/m^2$ whereas for green they were (0.127, 0.360) and $L = 57.6cd/m^2$. At low
136 saturation, the chromatic distance $d(u, v)$ between the two colors was $d(u, v) = 0.05$ and
137 the achromatic distance in terms of Michelson Contrast (MC) was $MC = 0.11$. At high
138 saturation, these values were $d(u, v) = 0.21$ and $MC = 0.388$. Hence, by changing color
139 saturation from 0.4 to 0.9, stimulus strength was increased significantly both in chromatic
140 and achromatic dimensions. It is also noteworthy that the chromatic distance values of 0.05
141 and 0.21 fall to the left and right of the critical distance $d(u, v) \approx 0.1$ at which the strength
142 of the chromatic stimulus for binocular rivalry starts to saturate as observed by Stalmeier
143 and de Weert (1998).

144 To allow for interocular grouping of complementary patches, the two halves with the same
145 orientation always shared the same color at the same saturation level, and were shown to
146 opposite hemifields of either eye. For example, the combination horizontal green/vertical red
147 presented to the left eye determined the combination vertical red/horizontal green presented
148 to the right eye, as well as the two grouped percepts – vertical red and horizontal green (See
149 Fig. 1B). In total, there were four possible stimulus arrangements, all completely determined

150 by any half of a stimulus presented to one eye. The two squares were displayed on a grey
151 background $(0.0, 0.0, 0.2)$: $(u, v) = (0.188, 0.442)$ and $L = 23.88\text{cd/m}^2$ and were contained
152 within a square frame with a protruding horizontal and vertical line to help image alignment.

153 *Experimental procedure.* Each session was divided into six 3-minute trials separated by a 90-
154 second resting period. To account for the time it took subjects to adjust to the stimuli and
155 form stable percepts, the first 30 seconds of each trial were not analyzed. The association
156 between color and orientation was maintained within a single session, but was randomized
157 across sessions. For example, we used a vertical red/horizontal green left eye stimulus across
158 some sessions (Fig. 1A). In contrast, saturation and the position of the horizontal grating
159 was randomized across the six trials. Within one session, each saturation level appeared in
160 three trials and each grating positioning occurred in three trials.

161 Four subjects finished 6 total sessions (AJ, MA, ZK, ND), three subjects finished 5 ses-
162 sions (FG, YW, ML), one subject finished 4 sessions (AB) and the remaining one finished 7
163 sessions (ZM). Therefore, after discarding the initial 30 seconds of each trial, a total of about
164 90 minutes of data over about 36 trials was collected per subject: about 18 trials for each
165 saturation conditions, with 3 trials per level and color/orientation pairing. See the Supple-
166 mentary Material which has been deposited to Github (<https://github.com/YunjiaoWang/multistableRivalry.git>) for more details.

168 Subjects were asked to indicate the dominant percept by holding down one of four dif-
169 ferent buttons (1, 2, 3, 4) on a gamepad. They were instructed to press button 1 when
170 perceiving a split grating with left part red; button 2 when perceiving split grating with left
171 part green; button 3 when perceiving an all red grating; and button 4 when perceiving an all
172 green grating. When the perceived image did not correspond to one of these four options,
173 subjects were instructed to release all buttons. **We also recorded the times during which**
174 **no stable percept was reported, and labeled them as “percept 0”.** Such a report typically
175 marked a transition between percepts, but could also be followed by a transition to the
176 same percept. Before the beginning of the experiment, subjects were familiarized with the
177 controller. The distribution of the times of different percepts, including no stable percepts,
178 and further details are presented in the Supplementary Material.

179 2.2. Data analysis

180 We performed the statistical analysis in R and provide a description of the analysis below.
181 Commented code, as well as all collected data are available in the Supplementary Material.

182 We conducted all data analyses under a Bayesian framework. Standard significance tests
183 would allow us to reject the null hypothesis that a color saturation change has no effect on
184 dominance time, but would not allow us to accept the alternative hypothesis. In contrast, a
185 Bayesian approach allows us to conclude that for some subjects a change in color saturation
186 did affect percept dominance. We believe that showing the probabilities that this effect
187 was present is more informative than concluding that a null hypothesis is rejected at some
188 (arbitrary) significance level. Our use of Bayesian statistics means that confidence intervals
189 are replaced by credible intervals, and traditional notions of “significance” do not apply.
190 Instead of using a fixed threshold for significance, we provide the probabilities that a change
191 in color saturation affects the perception of the stimuli, given the data (Wasserstein and
192 Lazar, 2016).

193 Importantly, in our analysis we use a hierarchical model to analyze concurrently the data
 194 from all subjects in the experiment (Gelman and Hill, 2006). Such models address the issue
 195 of multiple comparisons and provide efficient estimates (Gelman et al., 2012).

196 *Predominance of grouped percepts.* Using the time series recorded from each trial, we com-
 197 puted the predominance of grouped percepts. Predominance is the fraction of time that
 198 subjects reported a grouped percept, T_{grouped} , by pressing the corresponding gamepad but-
 199 ton, out of the total time they reported any percept (percepts 1, 2, 3 or 4), i.e.

$$r(i) = \frac{T_{\text{grouped}}(i)}{T_{\text{grouped}}(i) + T_{\text{single}}(i)}.$$

Here i is the number of the trial, with 18 trials at each color saturation level (0.4 and 0.9). This is equivalent to the fraction of time that buttons 3 or 4 were pressed out of the total time any button was pressed during trial i . In our analysis, we partitioned trials based on the color saturation level used for each trial, grouping across all other conditions. We analyzed changes in predominance using a linear Student- t regression model to account for skewness in the data. We included the condition (low/high color saturation) as a covariate and set the degrees of freedom of the t distribution to 4 to provide robust inference while avoiding computational difficulties often encountered when using a prior for the degrees of freedom (Fonseca et al., 2008). Letting r_{ij} be the predominance for subject j in trial i , the model is specified as:

$$\begin{aligned} r_{ij} &\sim t_4(\mu_{ij}, \sigma^2) \\ \mu_{ij} &= \beta_{0j} + \beta_{1j} x_{ij} \\ \beta_{0j} &\sim \text{Normal}(\beta_0, \tau_0^2), \beta_{1j} \sim \text{Normal}(\beta_1, \tau_1^2) \end{aligned} \tag{1}$$

200 where x_{ij} is the color saturation indicator (1 for 0.9, 0 for 0.4). The random regression
 201 coefficients β_{0j} and β_{1j} allow the effects of color saturation to vary across subjects. This hi-
 202 erarchical model assumes that the effects from different subjects are similar but not identical
 203 and come from the same population with overall means of β_0 and β_1 . Prior distributions
 204 for the overall saturation effects β_0 and β_1 were independent and normal with mean 0, and
 205 variance 10^4 . We used Uniform(0, 100) priors for the standard deviation of the random
 206 effects, τ_0 and τ_1 and Uniform(0, 1000) for σ . We estimated the mean difference in the
 207 fraction of time between the two saturation levels and its 95% credible interval (CI) and the
 208 probability that the difference is greater than 0. We performed an equivalent analysis to
 209 examine whether the mean dominance time of the single eye or grouped percepts changed
 210 across conditions.

From the i^{th} trial in each condition, we also computed ratios of the number of visits to grouped percepts, N_{grouped} , over the number of all visits to either single-eye or grouped percepts,

$$n(i) = \frac{N_{\text{grouped}}(i)}{N_{\text{grouped}}(i) + N_{\text{single}}(i)}.$$

211 We used the model specified in Eq. (1) to analyze $n(i)$ and determine the change in the
 212 fraction of visits to the grouped or single-eye percepts across conditions.

213 *Single-color images.* To examine the effect of saturation of the colors green and red individ-

214 ually we divided the grouped percepts into two sets – a set of all green (percept 4) and a
215 set of all red (percept 3). We then analyzed the effect of color saturation on predominance,
216 and dominance duration for each color individually using the same statistical approach and
217 models as in the case of grouped percepts.

Transition probabilities. To estimate the transition probabilities between percept types, we classified percepts into two states: single-eye, S , corresponding to percepts 1 and 2, and grouped, G , corresponding to percepts 3 and 4. For each trial, we converted the data into two binary sequences: One sequence contained all transitions from state S with transitions from S to S denoted by 1, and from S to G by 0. The second sequence contained transitions from G , those from G to G denoted by 1, and from G to S by 0. We used all data obtained by each subject in a given condition (low/high color saturation) to estimate the transition probability from S to S , and from G to G . The model is specified as

$$\begin{aligned} y_{ij} &\sim \text{Bernoulli}(p_{ij}) \\ p_{ij} &= \theta_{0j} + \theta_{1j} x_{ij} \\ \theta_{0j} &\sim \text{Beta}(\omega * (\kappa - 2) + 1, (1 - \omega) * (\kappa - 2) + 1), \theta_{1j} \sim \text{Normal}(\theta_1, \tau_1^2) \end{aligned} \quad (2)$$

218 where x_{ij} is the color saturation indicator (1 for 0.9, 0 for 0.4). We used vague priors: a
219 uniform prior on the interval $[0, 1]$ for the mode, ω , and a Gamma prior with rate and shape
220 both equal to 0.01 for the concentration parameter, κ . Prior distributions for the overall
221 saturation effects θ_1 was independent of these, and normal with mean 0, and variance 10^4 .
222 We used Uniform(0, 100) prior for the standard deviation of the random effect τ_1 .

223 *Model implementation.* All Bayesian models were implemented via Markov Chain Monte
224 Carlo methods in JAGS. We used 3 MCMC chains with at least 20,000 iterations after an
225 initial burn-in of 4000 iterations. We assessed convergence by calculating the Gelman-Rubin
226 diagnostic, \hat{R} for all parameters.

227 3. Results

228 Nine observers were presented with two split-grating images simultaneously to each eye
229 using a haploscope (See Methods). Subjects reported one of four possible percepts by press-
230 ing buttons on a game pad. We examined how the fraction of time subjects perceived
231 grouped images (the *predominance* of grouped images) depended on color saturation.

232 *Dominance durations follow a gamma distribution.* The dominance duration, the total time
233 that a subject reported seeing a percept for single-eye and grouped percepts had the shape
234 of a gamma distribution (See Fig. 2 and Supplementary Material.) This is consistent with
235 previous studies of perceptual multistability (Blake and Logothetis, 2002; Brascamp et al.,
236 2005; van Ee, 2009).

237 For some, but not all subjects, the mean of single-eye percept times decreased with an
238 increase in color saturation (Fig. 2). A more thorough analysis was therefore needed to
239 determine the effect of color saturation on percept predominance.

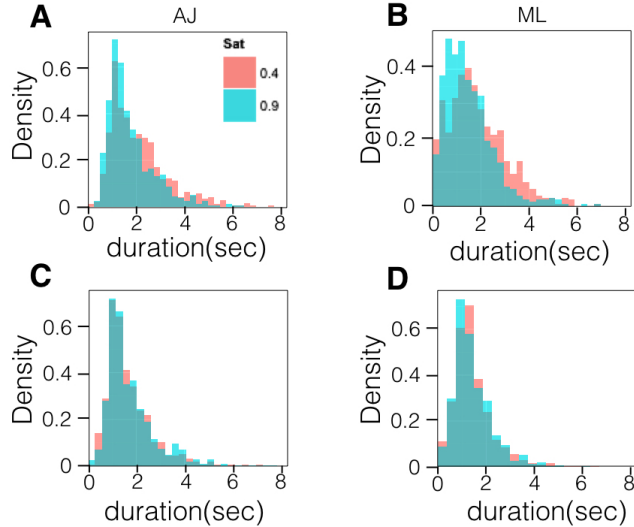
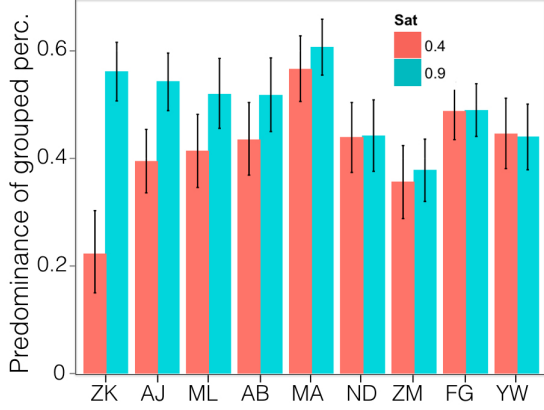


Figure 2: Dominance times for two subjects, ML and AJ, approximately follow a gamma distribution. (A,B) Histograms of single-eye percept durations are unimodal, but somewhat different between the two saturation conditions. (C,D) Histograms of the grouped percept durations are closer to each other. Each histogram contains data collected from 18 trials of 2.5 minutes each, amounting to approximately 1200 dominance duration reports (See Methods and Supplementary Material for more details).

240 *Predominance of grouped percepts.* We first examined whether an increase in color saturation
 241 affected the fraction of time grouped percepts were reported. We hypothesized that
 242 predominance of grouped percepts increases with color saturation, as a result of a stronger
 243 visual cue to bind the two complementary halves of the stimuli presented to each eye into a
 244 coherent percept (Wagemans et al., 2012). The data supports this in five out of nine subjects
 245 (Fig. 3): For five out of the nine subjects there was a 0.92 or higher probability that the
 246 difference in mean predominance times increased with color saturation given the reported
 247 observations (See Table in Fig. 3). This is in accord with Levelt’s Proposition I, as color
 248 saturation, increases predominance. There was no evidence that changes in color saturation
 249 impacted predominance in the remaining subjects.

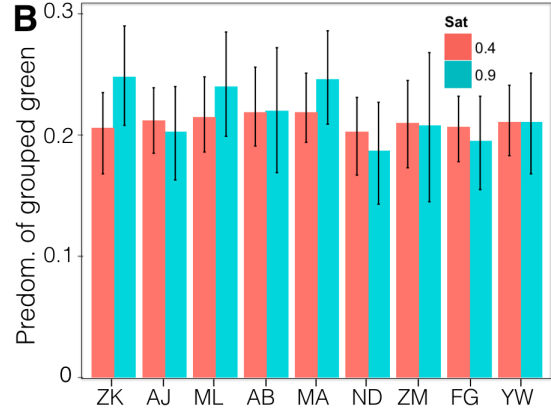
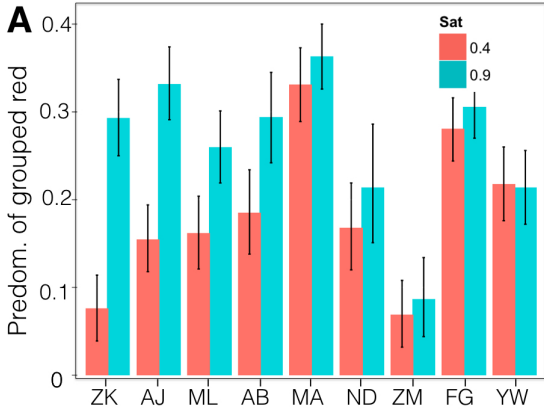
250 We also examined predominance of grouped red and grouped green percepts separately,
 251 and found much larger changes for the grouped red percepts (Fig. 4). This cannot be ex-
 252 plained by a strengthening of luminance or image contrast, since at high saturation the green
 253 color has higher luminance. A similar trend holds for achromatic contrast (See Methods).
 254 However, in several contexts the color red tends to be a more salient than green (Emmanouil
 255 et al., 2013; Stromeyer and Eskew., 1992; Lindsey et al., 2010). Red images may promote
 256 a strong top-down attention signal from higher order areas processing object color (Had-
 257 jikhani et al., 1998). Furthermore, unlike single-eye percepts, the predominance of grouped
 258 green percept does not decrease. This suggests the strength of the grouped green percepts
 259 increases with color saturation, but to a smaller degree than for the red percepts. If the
 260 strength of the grouped green percept did not increase, we would expect its predominance
 261 to decrease, as for single-eye percepts (Fig. 3).

262 We next examined how this change in predominance was related to both changes in
 263 average dominance time and the frequency of visits to single-eye versus grouped percepts.



ID	diff.	95% CI	prob.
ZK	0.31	(0.20, 0.41)	0.999
AJ	0.14	(0.06, 0.22)	0.999
ML	0.11	(0.02, 0.20)	0.989
AB	0.09	(-0.01, 0.18)	0.966
MA	0.06	(-0.02, 0.13)	0.928
ND	0.01	(-0.09, 0.10)	0.550
ZM	0.01	(-0.07, 0.10)	0.629
FG	0.01	(-0.06, 0.08)	0.597
YW	-0.00	(-0.09, 0.08)	0.489

Figure 3: (Plot) Grouped percept predominance: each colored bar indicates the mean predominance at a given color saturation level in a given subject and black error bars denote the 95% credible intervals. (Table) Differences between ratios at the two color saturation levels: diff. = difference of predominance means at saturation 0.9 and 0.4; 95% CI stands for 95% credible interval; ‘prob.’ is the probability that the predominance of grouped percepts is higher at saturation level 0.9 (See Methods). We use the same ordering of subjects in all subsequent tables and figures, so that the five subjects sensitive to changes in color saturation are listed first.



grouped red				grouped green			
ID	diff.	95% CI	prob.	ID	diff.	95% CI	prob.
ZK	0.22	(0.16, 0.28)	0.999	ZK	0.04	(-0.01, 0.10)	0.955
AJ	0.18	(0.12, 0.23)	0.999	AJ	-0.01	(-0.06, 0.03)	0.353
ML	0.10	(0.04, 0.15)	0.999	ML	0.03	(-0.02, 0.08)	0.848
AB	0.11	(0.04, 0.18)	0.999	AB	0.00	(-0.06, 0.05)	0.530
MA	0.03	(-0.02, 0.09)	0.876	MA	0.03	(-0.01, 0.07)	0.885
ND	0.05	(-0.03, 0.13)	0.878	ND	-0.02	(-0.07, 0.03)	0.262
ZM	0.02	(-0.04, 0.08)	0.738	ZM	-0.00	(-0.07, 0.06)	0.499
FG	0.03	(-0.03, 0.08)	0.836	FG	-0.01	(-0.06, 0.03)	0.301
YW	-0.01	(-0.06, 0.05)	0.439	YW	-0.00	(-0.05, 0.04)	0.498

Figure 4: Predominance of grouped green and grouped red percepts: (A) grouped red percept: there is a pronounced increases in predominance with the color saturation in the first six subjects with probability around 0.9. (B) grouped green percept: predominance is largely unchanged, with two subjects (ZK, MA) showing a slight increase.

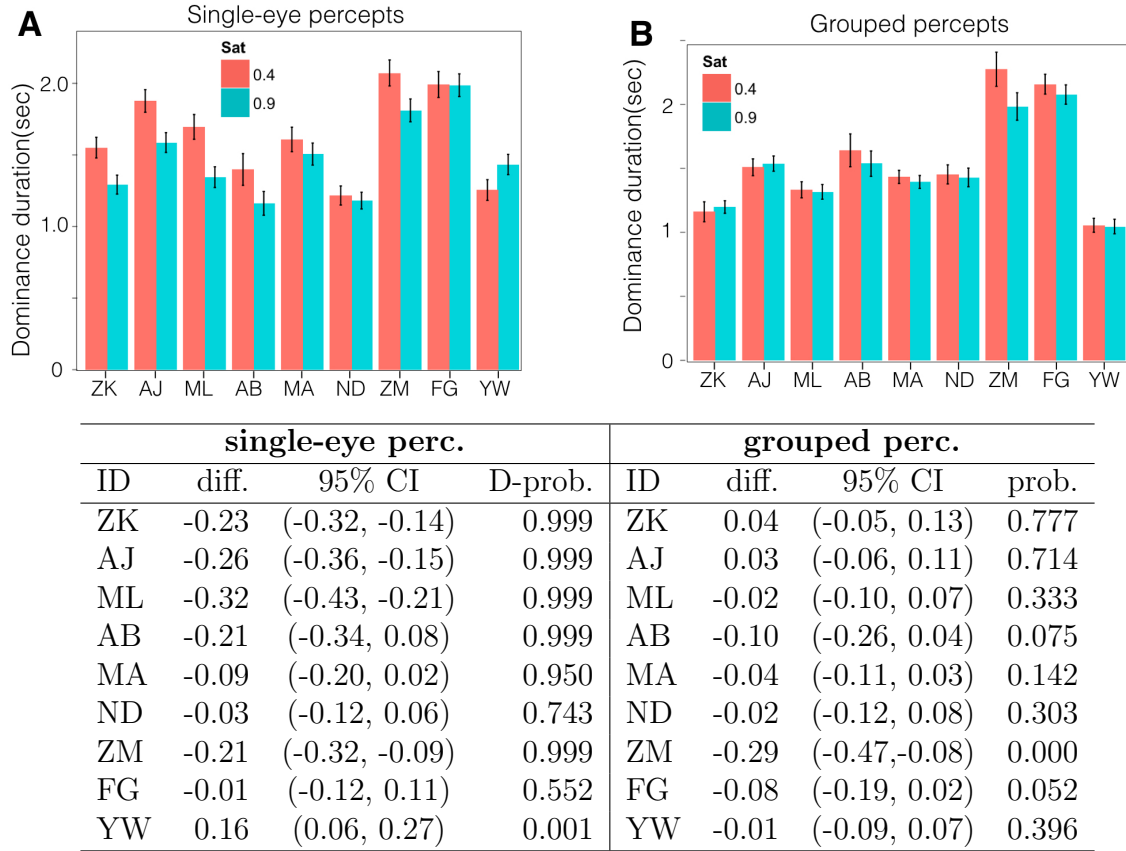


Figure 5: Average dominance durations: (A) single-eye percepts and (B) grouped percepts. Single-eye percept dominance durations decrease as color saturation is increased for the subjects who also experience increased grouped percept predominance. Here ‘D-prob.’ (on left) is the probability that the dominance duration of single-eye percepts decreases and ‘prob.’ (on right) is the probability that the dominance duration of grouped percepts increases.

264 3.1. Causes of predominance changes

265 In the case of only two percepts, the number of visits to each percept will differ by at most
 266 one per trial (van Ee, 2009), and dominance duration is closely related to predominance.
 267 When there are more than two percepts, they do not simply alternate, and the order in
 268 which multiple percepts appear can affect predominance (Naber et al., 2010; Huguet et al.,
 269 2014). Thus, to understand changes in predominance we must examine how color saturation
 270 influences dominance duration, as well as the number of visits to each percept.

271 *Single-eye percept durations decrease with color saturation.* We compared the average dom-
 272 inance durations of single-eye and grouped percepts for the two different color saturation
 273 conditions in Fig. 5. In six out of nine subjects, there was a higher than 0.95 probability that
 274 dominance duration of single-eye percepts decreased as color saturation increased (subjects
 275 ZK, AJ, ML, AB, MA, ZM, See Fig. 5A). These included the five subjects for which the
 276 predominance of grouped percepts increased. There was no strong evidence that increased
 277 color saturation increased the dominance duration of all grouped percepts in any subjects.

278 The generalization of Levelt’s Proposition II states that increasing the difference between
 279 the percept strength of grouped and single-eye percepts increases the average perceptual

280 dominance duration of the stronger percepts Brascamp et al. (2015). By increasing color
281 saturation, we decreased the difference in stimulus strength between single-eye and grouped
282 percepts: In the low color saturation case, the single-eye percepts were stronger, as their
283 predominance was higher than that of grouped percepts (Fig. 3, for seven of the nine subjects
284 the predominance of grouped percepts was below 0.5 with a probability of 0.94 or higher.
285 See Supplementary Material). At higher color saturation the grouped percepts had a mean
286 predominance of near 0.5 or below for eight subjects. We therefore concluded that the
287 single-eye percepts are stronger. Thus, for most subjects who were sensitive to a change
288 in percept strength the stronger percepts' (single-eye) mean dominance duration decreased,
289 while the weaker percepts' (grouped) durations remained roughly the same. We explore
290 further comparisons with Propositions II-IV in the Discussion.

291 A separate analysis of dominance duration changes of the grouped green and red percepts
292 shows that changes are less pronounced than those of single-eye percepts (Fig. 6): There is a
293 slight increase in the dominance duration of the grouped red percept, but this is in line with
294 Proposition II, which allows for slight increases in the dominance duration of percepts whose
295 stimulus strength increases (Brascamp et al., 2015). Furthermore, the slight decrease in the
296 dominance duration of grouped green percepts is smaller than the decrease for single-eye
297 percepts. We can see this by looking at the probabilities: the average dominance duration
298 of the single-eye percepts in the first five subjects showed decreases with > 0.95 probability
299 while that of either all green or all red demonstrated changes with such high probability only
300 in two subjects out of these five subjects. Thus, in line with Proposition II, the substantial
301 increase in the predominance of the grouped red percept is accompanied by a slight to no
302 increase in the dominance duration.

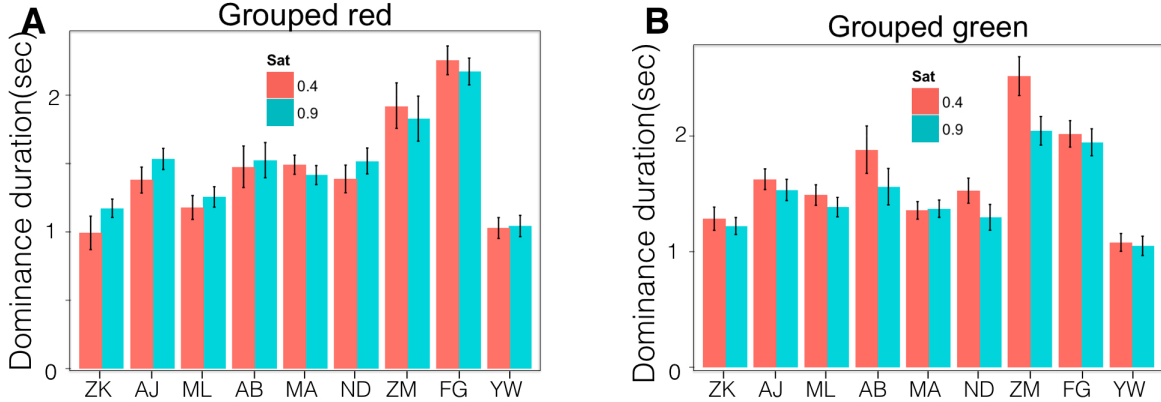
303 *Grouped percept visit frequency increases with color saturation.* With multiple percepts, each
304 can occur with a frequency between 0% to 50%, excluding self-transitions. This frequency
305 impacts predominance (Naber et al., 2010; Huguet et al., 2014). We therefore examined
306 how the frequency of visits to single-eye and grouped percepts depended on color saturation.
307 Consistent with our results for grouped percept predominance (Fig. 3), the frequency of visits
308 to grouped percepts increased with color saturation in most subjects (Fig. 7, see Methods
309 for details about the analysis): Subjects ZK, AJ, ML and AB (probability > 0.94), and to
310 a lesser degree MA (prob. > 0.82), show a consistent increases in the number of visits to
311 grouped percepts.

312 We conclude that two main factors contributed to increased predominance of grouped
313 percepts: the average dominance duration of single-eye percepts decreased, while the dom-
314 inance durations of grouped percepts remained approximately unchanged, and the grouped
315 percepts were visited more frequently when color saturation was high.

316 3.2. Transitions to grouped percepts increase with color saturation

317 We also analyzed the transition probability between percepts. We focused on the fre-
318 quency of transitions between each percept type: single-eye or grouped percepts (See Fig.
319 8A). In doing so, we reduced the number of possible transitions to four: single-eye to grouped,
320 grouped to single-eye, grouped to grouped, and single-eye to single-eye (See Methods).

321 Our analysis of the frequency of visits to grouped percepts (Fig. 7) suggests an increase in
322 transitions to grouped percepts in the high color saturation condition. Consistent with this
323 trend, we found that the ratio of transitions from single-eye to single-eye percepts decreased



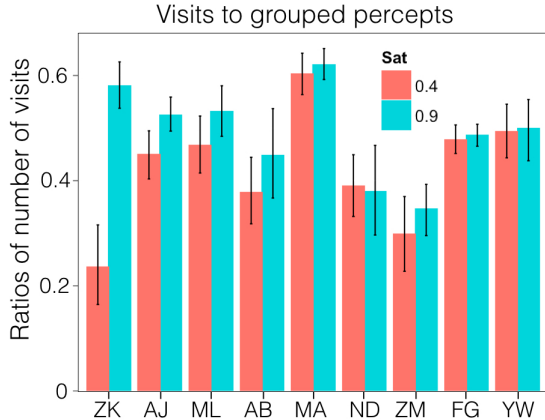
grouped red				grouped green.			
ID	diff.	95% CI	prob.	ID	diff.	95% CI	D-prob.
ZK	0.18	(0.04, 0.32)	0.997	ZK	-0.06	(-0.18, 0.06)	0.843
AJ	0.15	(0.04, 0.27)	0.995	AJ	-0.09	(-0.22, 0.03)	0.929
ML	0.08	(-0.03, 0.19)	0.915	ML	-0.10	(-0.22, 0.02)	0.956
AB	0.05	(-0.13, 0.22)	0.713	AB	-0.32	(-0.57, -0.09)	0.998
MA	-0.07	(-0.17, 0.02)	0.062	MA	0.01	(-0.09, 0.12)	0.394
ND	0.13	(0.00, 0.27)	0.976	ND	-0.23	(-0.38, -0.08)	0.999
ZM	-0.09	(-0.32, 0.10)	0.204	ZM	-0.47	(-0.68, -0.26)	0.999
FG	-0.08	(-0.22, 0.05)	0.126	FG	-0.07	(-0.23, 0.08)	0.819
YW	0.01	(-0.09, 0.12)	0.605	YW	-0.03	(-0.14, 0.08)	0.716

Figure 6: The average dominance duration of grouped red shows increases in some subjects and grouped green on the other hand demonstrates decreases in several subjects. However, the magnitude of the changes overall are less pronounced as that in single-eye percepts.

324 in the first five subjects (ZK, AJ, ML, MA, and ZM in Fig. 8B). This implies that the ratio
 325 of the transitions from single-eye to grouped percepts increased as color saturation increased.
 326 In addition, the ratio of grouped percepts to grouped percepts transitions increased as the
 327 color saturation for four out of those five subjects ($\text{prob} > 0.94$, see Fig. 8C). Thus, there was
 328 an increase in the frequency of transitions between grouped percepts. This phenomenon has
 329 previously been referred to as “trapping”, as it suggests a subject’s perception is trapped in
 330 a subset of all possible percepts (Suzuki and Grabowecky, 2002).

331 4. Discussion

332 Multistable perceptual phenomena have long been used to probe the mechanisms under-
 333 lying visual processing (Leopold and Logothetis, 1999). While binocular rivalry is used most
 334 frequently (Blake and Logothetis, 2002), different insights can be obtained by employing
 335 visual inputs that are integrated to produce interocularly grouped percepts (Kovacs et al.,
 336 1996; Suzuki and Grabowecky, 2002). These experiments are particularly informative when
 337 guided by Levelt’s Propositions, originally developed in the case of binocular rivalry (Levelt,
 338 1965; Brascamp et al., 2015). Here we used this approach to identify how color saturation
 339 influences the dynamics of perceptual multistability involving interocular grouping.



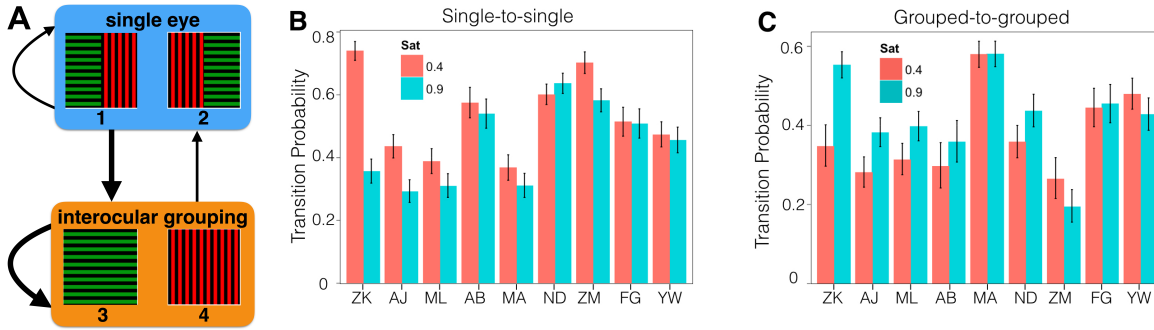
ID	diff.	95%CI	prob.
ZK	0.32	(0.25, 0.39)	0.999
AJ	0.08	(0.02, 0.14)	0.996
ML	0.07	(0.00, 0.13)	0.975
AB	0.06	(-0.01, 0.14)	0.948
MA	0.03	(-0.03, 0.08)	0.829
ND	-0.01	(-0.09, 0.06)	0.351
ZM	0.04	(-0.03, 0.10)	0.873
FG	0.01	(-0.05, 0.07)	0.630
YW	0.02	(-0.05, 0.08)	0.700

Figure 7: Frequency of visits to grouped percepts out of all visits. The mean increases for eight out of nine subjects when color saturation is increased from 0.4 to 0.9. The five subjects who experienced an increase in grouped percept predominance, also showed an increase in the frequency grouped percept visits. Values in the table are computed in the same way as in Fig. 3.

340 *Related work.* We showed that multiple cues (color and collinearity) affect interocular group-
341 ing. Varying color saturation, we were able to show that color impacts the dominance of
342 integrated images in accordance with a generalization of Levelt’s propositions. Alais and
343 Blake (1999) studied the impact of orientation on the predominance of grouped stimuli
344 when percept halves originated from the same eye. Stuit et al. (2011, 2014) explored a
345 paradigm related to our own with the orientation of complementary image halves impacting
346 interocular grouping. While they identified orientation as a cue for interocular grouping, the
347 increase in predominance was not analyzed in detail. Zhaoping and Meng (2011) considered
348 the role of color in Dichoptic completion, rather than binocular rivalry. Nothdurft (1993)
349 investigated the role of different visual object features (orientation, motion, and color) in the
350 detection of objects, finding that color did facilitate object detection. Our results are more
351 closely related to the work by Kim and Blake (2004) and Kovacs et al. (1996). Kovacs et al.
352 (1996) showed that color promotes interocular grouping: they obtained evidence for stable
353 and relatively long percepts in which all the elements appeared to be of one color (all-red or
354 all-green). However, neither study examined the underlying causes of these effects or how
355 they extend to Levelt’s propositions to multistable perceptual rivalry involving interocular
356 grouping.

357 *Color saturation facilitates grouping of complementary image halves.* We demonstrated that
358 increasing the color saturation of ambiguous visual inputs can increase the predominance of
359 grouped percepts. This is consistent with the Gestalt law of similarity (Wagemans et al.,
360 2012). While this effect tended to be strongest for the grouped red percept, we did find
361 evidence that the grouped green percept became more salient than in the low color satura-
362 tion condition. The neural mechanisms underlying collinear facilitation for chromatic and
363 achromatic contours appear to be different (Beaudot and Mullen, 2003; Huang et al., 2007),
364 suggesting that multiple channels in the visual system affect the grouping of image halves.
365 We propose that color provides one cue that promotes the grouping of objects between eyes.

366 *Inter-subject Variability.* It is important to note that we only observed an appreciable in-
367 crease in grouped percept predominance in five out of nine subjects (Fig. 3). In the remaining



single-to-single				grouped-to-grouped			
ID	diff.	95% CI	D-prob.	ID	diff.	95% CI	prob.
ZK	-0.37	(-0.42, -0.32)	0.999	ZK	0.19	(0.12, 0.25)	0.999
AJ	-0.14	(-0.19, -0.09)	0.999	AJ	0.09	(0.04, 0.15)	0.999
ML	-0.08	(-0.13, -0.03)	0.998	ML	0.08	(0.03, 0.13)	0.999
AB	-0.04	(-0.10, 0.03)	0.868	AB	0.06	(-0.01, 0.13)	0.941
MA	-0.06	(-0.12, -0.01)	0.985	MA	0.01	(-0.04, 0.05)	0.640
ND	0.03	(-0.01, 0.08)	0.087	ND	0.08	(0.02, 0.13)	0.996
ZM	-0.12	(-0.17, -0.07)	0.999	ZM	-0.06	(-0.12, 0.00)	0.032
FG	-0.01	(-0.08, 0.05)	0.645	FG	0.02	(-0.05, 0.08)	0.712
YW	-0.02	(-0.08, 0.04)	0.774	YW	-0.04	(-0.10, 0.02)	0.089

Figure 8: (A) Diagram showing the case where single-to-single percept transitions are less likely than grouped-to-grouped transitions, represented by the thickness of transition arrows. (B,C) The probability of transitions from (B) single-to-single percepts, and (C) grouped-to-grouped percepts. The probability of a single-to-single transition tends to decrease with color saturation whereas the grouped-to-grouped transition probability tends to increase in the cohort of subjects whose grouped predominance increased. The table gives the posterior probability of a decreases in single-to-single transition, and an increase in grouped-to-grouped transitions given the data.

368 four subjects we did not observe an effect of color saturation on percept predominance. One
369 possible reason for this result is that subjects differed in their sensitivity to color satura-
370 tion (Kaiser and Boynton, 1996). Although no subjects reported problems with distinguish-
371 ing colors, they may have responded differently if the change in color saturation was larger,
372 or if we used different colors. For example, the wide array of sensitivities to contrast across
373 human subjects are reflected in the range of mean dominance time durations in binocular
374 rivalry (Bossink et al., 1993; Brascamp et al., 2006; van Ee, 2009). Also, the relationship be-
375 tween color saturation and percept predominance is likely nonlinear Stalmeier and de Weert
376 (1998). The color saturation values we used may have fallen in the flat portion of the
377 function that describes the relation between color saturation and predominance for the four
378 unaffected subjects.

379 As mentioned previously, Stalmeier and de Weert found significant inter-subject variabil-
380 ity even when isoluminance points were calibrated individually for each subject (Stalmeier
381 and de Weert, 1998). The effect of chromatic signal strength on binocular rivalry depended
382 both on the calibration criterion (flicker photometry versus MDB) and the direction along
383 which colors are sampled in the color space. (Stalmeier and de Weert, 1998) also showed sig-
384 nificant inter-subject variability both in the absolute effectiveness of achromatic contrast and

385 its relative effectiveness with respect to chromatic contrast (Stalmeier and de Weert, 1998).
386 Inter-subject variability has been reported in relatively low-level tasks (e.g. Halpern et al.
387 (1999)), as well as in multistable perception (Kleinschmidt et al., 2012), which is interpreted
388 to include both low-level and high-level factors. Hence, for future studies, we suggest the use
389 of multiple levels of the percept-strength variable in order to characterize more completely
390 the performance of each subject individually. In addition, it would help us identify the rela-
391 tive contributions of color saturation and luminance to percept strength, since red and green
392 have different luminance at a fixed saturation (See Methods). This would provide a test for
393 the generality of our conclusions, and this would also help us to identify stronger instances
394 of grouping for the grouped green percept. Increasing the number of subjects would allow
395 us to better characterize inter-subject variability, but would likely not make it disappear.

396 *Extending Levelt’s propositions to interocular grouping.* Interocular grouping has been re-
397 ported with different sets of patchwork images (Kovacs et al., 1996; Suzuki and Grabowecky,
398 2002). However, earlier studies did not quantify specific ways in which a stimulus parameter
399 could affect the predominance of grouped images. We have shown that color saturation used
400 as a grouping cue differentially controls the strength of single-eye and grouped percepts, and
401 increasing color saturation can increase grouped percept predominance. As this effect was
402 strongest for all red percept, it suggests that color saturation, and particularly that of the
403 color red, may act as a stimulus strength parameter for grouped percepts.

404 In agreement with Proposition II, the predominance of single-eye percepts was higher
405 at low color saturations, and their dominance durations decreased in the higher color satu-
406 ration condition, while the overall dominance duration of grouped percepts did not change
407 much. Proposition III then follows from Proposition II. Finally, since we could not deter-
408 mine whether we equally increased the strength of both single-eye and grouped percepts, it
409 is unclear whether our results are consistent with Levelt Proposition IV. Color saturation
410 may affect monocular and binocular integration in different ways (Sincich and Horton, 2005).
411 Stimulus parameter changes obeying Proposition IV would have to keep predominance fixed,
412 while decreasing mean dominance durations.

413 Studies of interocular grouping in perceptual multistability have a long history (Diaz-
414 Caneja, 1928). We focused on split single-eye images for simplicity, but we anticipate that
415 our findings extend to the patchwork images of Kovacs et al. (1996). The simple grating-
416 based inputs we used were more similar to the geometric images of Suzuki and Grabowecky
417 (2002). We expect that our findings extend to achromatic images as long as a parameter
418 can be identified that affects grouped percept predominance. For example, we could use
419 achromatic textures as a cue to group complementary stimulus halves. In general, we suggest
420 that our findings apply to any stimulus feature that promotes grouping along the lines of
421 Gestalt laws of grouping.

422 *Neural mechanisms of perceptual multistability.* Our observations support the prevailing the-
423 ory that perceptual multistability is significantly percept-based and involves higher visual
424 and object-recognition areas (Leopold and Logothetis, 1999). Since the first systematic study
425 on binocular rivalry (Wheatstone, 1838), much work has been devoted to identifying its un-
426 derlying neural mechanisms: Mutual inhibition allows for the selection of one percept among
427 many (Lumer, 1998; Tong and et al, 1998; Tong, 2001; Lee et al., 2005; Haynes et al., 2005;
428 Meng et al., 2005; Moutoussis et al., 2005; Wunderlich et al., 2005; Seely and Chow, 2011),
429 adaptation can lead to switching between percepts (Kim et al., 2006; Brascamp et al., 2006;

430 van Ee, 2009), and neuronal noise accounts for the irregularity of perceptual dominance
431 intervals (Brascamp et al., 2006; Moreno-Bote et al., 2007; Shpiro et al., 2009; Lankheet,
432 2006). However, a number of issues remain unresolved. Activity predictive of a subject’s
433 dominant percept has been recorded in lateral geniculate nucleus (LGN) (Haynes and Rees,
434 2005), primary visual cortex (V1) (Lee and Blake, 2002; Polonsky et al., 2000), and higher
435 visual areas (e.g., V2, V4, MT, IT) (Logothetis and Schall, 1989; Leopold and Logothetis,
436 1996; Sheinberg and Logothetis, 1997). Thus, rivalry likely results from interactions between
437 networks at several levels of the visual system (Freeman, 2005; Wilson, 2003; Dayan, 1998).

438 Collinear facilitation involves both recurrent connectivity in V1 as well as feedback con-
439 nections from higher visual areas like V2 (Angelucci et al., 2002; Gilbert and Sigman, 2007),
440 reenforcing the notion that perceptual rivalry engages a distributed neural architecture. How-
441 ever, a coherent theory that relates image features to dominance statistics during perceptual
442 switching is lacking. It is unclear how neurons that are associated to each subpopulation
443 may interact due to grouping factors such as collinearity and color.

444 *Conclusion.* Our work supports the general notion that perceptual multistability is a dis-
445 tributed process that engages several layers of the visual system. Interocular grouping re-
446 quires integration in higher visual areas (Leopold and Logothetis, 1996), but orientation pro-
447 cessing and competition occurs earlier in the visual stream (Angelucci et al., 2002; Gilbert
448 and Sigman, 2007). Furthermore, the fact that color saturation can modulate the statistics
449 of perceptual multistability provides a novel stimulus parameter that can be varied in visual
450 inputs to probe the neural mechanisms of visual integration and competition.

451 5. Acknowledgments

452 Gemma Huguet and Ruben Moreno-Bote provided helpful comments. Funding was pro-
453 vided by NSF-DMS-1311755 (ZPK); NSF-DMS-1517629 (KJ and ZPK); and NSF-DMS-
454 1122094 (KJ). YW was supported by DHS-2014-ST-062-000057 and by a seed grant from
455 Texas Southern University.

456 Supplementary material can be found at <https://github.com/YunjiaoWang/multistableRivalry.git>

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